THE NORTH AMERICAN SPECIES OF VULPIA (GRAMINEAE)

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The grass genus *Vulpia* comprises approximately 25 species native to temperate and subtropical regions of Europe, the Mediterranean region, and North and South America. Several species have been introduced into Asia and Australia. In the warmer regions these grasses grow only during the cool season or at high elevations. Of the five North American species two are introduced and the others are native.

Piper (1906), Hitchcock (1935), and Chase (1951) grouped the American species of *Vulpia* in *Festuca*. Others, including Bews (1929), Henrard (1937), Fernald (1945, 1950), Chippendall (1955), Parodi (1956), Paunero (1964), Hubbard (1968), and Rosengurtt et al. (1970) have accorded *Vulpia* generic rank.

The present investigation was undertaken to determine the taxonomic relationships of the five species of *Vulpia* native to or adventive in North America. Of special concern were patterns of variation within populations of the widespread west coast species, *V. microstachys*.

Gross Morphology

Species of *Vulpia* characteristically are short-lived annuals. Morphological characters selected as having most diagnostic value in the delimitation of species are the general conformation of the inflorescence (pedicels and panicle branches erect or spreading), spikelet length, number of florets per spikelet, relative lengths of the glumes, length of the lowermost floret, and length of the lemma awn of lowermost floret. Spikelet indument is the primary character utilized in the delimitation of varieties.

Anatomy — Histology

In transverse section the culm internodes of the five species of *Vulpia* examined follow the general cellular pattern described by Metcalfe (1960) for *Festuca arundinacea* Schreb. The internodes have a large central cavity bordered by thin-walled parenchyma cells. Vascular bundles are arranged in an outer ring of small bundles embedded in the sclerenchyma of the cortex and an inner ring of larger bundles located in the ground tissue of the "pith" area. Surrounding all vascular bundles is a single ring of sheath cells.

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Examination of the internal anatomy of the leaf blade of the five North American species of *Vulpia* confirmed previous reports that these are "festucoid". In all material examined the bundle sheaths are double, with the cell walls of the inner sheath radially thickened. The outer sheath cells are large and thin-walled. Chlorenchyma cells of the mesophyll are loosely and irregularly arranged. Clusters of small, thick-walled sclerenchyma cells are associated both adaxially and abaxially with the larger vascular bundles of the leaf. Sclerenchyma cells are not associated with the smaller vascular bundles.

The adaxial blade surface exhibits well developed ribs. Each rib is comprised of a single vascular bundle and associated supporting cells. The vascular bundles are separated by deep U-shaped furrows. Bulliform cells at the base of the furrow are fan-shaped in *V. myuros* var. *hirsuta, V. bromoides,* and *V. octoflora* var. *octoflora,* irregular in varieties of *V. microstachys,* and only slightly different from other epidermal cells in *V. myuros* var. *myuros.* Differences in bulliform cells provide a diagnostic feature for separation of *V. myuros* var. *myuros* from *V. myuros* var. *hirsuta.*

Leaf epidermis features of *Vulpia* taxa were found to be typically festucoid and essentially the same as for the species of *Festuca* reported on by Metcalfe (1960). The short cells in the epidermis over the vascular bundles are solitary or paired, microhairs are absent, and the silica bodies are round or elliptical. The silica cells generally are adjacent to cork cells and appear to fit into concavities in the thick-walled cork cells. Long cells in the intercostal region have slightly sinuous walls. Stomata predominantly are on the abaxial surface and are generally arranged in regular rows. Subsidiary cells of the stomata are dome-shaped. The leaf epidermis of *V. sciurea* is noticeably different from that of the other species studied in that the stomata are relatively more abundant and the long cells of the intercostal zones are narrower.

Cytology

The basic chromosome number for *Vulpia* is $x = 7$. All North American species are either diploid ($2n = 14$) or hexaploid ($2n = 42$), but several European species have been reported to be tetraploid ($2n = 28$). Aneuploidy has not been reported for the genus.

Previous chromosome records for taxa present in North America are as follows: *Vulpia bromoides,* $2n = 14$, Stahlin, in Darlington and Wylie, 1956, Myers, 1947, Löve and Löve, 1948, Hedberg, 1957; *V. octoflora* var. *octoflora,* $2n = 14$, Gould, 1958; *V. octoflora* var. *hirtella,* $2n = 14$, Bowden and Senn, 1962; *V. myuros* var. *myuros,* $2n = 14$, Litardiere, in Darlington and Wylie, 1956; $2n = 42$, Litardiere, 1950, Gould 1966; *V. myuros* var. *hirsuta,* $2n = 42$, Gould, 1960, reported as *Festuca megalura; V. microstachys,* $2n = 42$, Niehaus, 1961, counts for plants referable to all recognized varieties of the species.

The following 38 chromosome counts were made in the present study. Counts for *Vulpia sciurea, V. microstachys* var. *pauciflora,* and *V. m.* var. *ciliata* were from mitotic preparations, all others were from meiotic divisions. The record for *V. sciurea* is the first for the taxon. Unless otherwise indicated, the collections cited are those of R. I. Lonard. Voucher specimens are deposited in TAES.

Vulpia octoflora var. *octoflora.* $2n = 14$. Oklahoma. Logan Co.: *2311.* Texas. Brazos Co.: *1888.* Henderson Co.: *2300.* Jasper Co.: *2092.* Leon Co.: *2056, 2108.* Liberty Co.: *2079.* Newton Co.: *2089.* Robertson Co.: *2054, 2107.* Van Zandt Co.: *2070.*

Vulpia octoflora var. *glauca.* $2n = 14$. Kansas. Chase Co.: *2376.* Jefferson Co.: *2359.* McPherson Co.: *2322.* Reno Co.: *2336.* Texas. Austin Co.: *2015.* Kendall Co.: *Waller 1923.* Llano Co.: *2204.* Mason Co.: *Waller 1899.*

Vulpia octoflora var. *hirtella,* $2n = 14$. Arizona. Graham Co.: *2268.* Pinal Co.: *2249.* Santa Cruz Co.: *2220.* Texas. Atascosa Co.: *2273.* Wilson Co.: *2022.*

Vulpia sciurea. $2n = 42$ (mitotic preparations). Texas. Bexar Co.: *Waller 1929.* Brazos Co.: *2197.*

Vulpia myuros var. *myuros.* $2n = 42$. Texas. Angelina Co.: *2095.* Bowie Co.: *2116.* Cherokee Co.: *2074.* Hunt Co.: *2121.* Leon Co.: *2109.* Van Zandt Co.: *2067.*

Vulpia myuros var. *hirsuta.* $2n = 42$. Texas. Brazos Co.: *2075.* Hopkins Co.: *2120.* Marion Co.: *2114.*

Vulpia microstachys var. *simulans.* $2n = 42$ (mitotic preparations). Arizona. Pinal Co.: *2254.* Gila Co.: *2258.*

Vulpia microstachys var. *ciliata.* $2n = 42$ (mitotic preparations). Arizona. Graham Co.: *2269.*

Taxonomy

Vulpia K.C. Gmelin, Fl. Baden. 1:8. 1805. Type species: *Vulpia myuros* (L.) K.C. Gmelin.—*Festuca* L. subg. *Vulpia* (K.C. Gmelin) Hackel, in Engler and Prantl, Nat. Pflanzenfam. 2:75. 1887.

Annuals (the North American species), with weak, erect or decumbent culms, these branching only or mainly at the base. Sheaths rounded, glabrous or pubescent. Ligules membranous, usually less than 1 mm long. Blades thin, narrow, flat or loosely involute. Inflorescence a narrow panicle with stiff, appressed or spreading branches or reduced to a spicate raceme. Spikelets laterally compressed, with (1–) 2–17 florets, the uppermost reduced. Disarticulation above glumes and between florets. Glumes subulate, the first 1-nerved, the second 3-nerved. Lemmas lanceolate or acuminate, 5-nerved, mucronate or with an awn to 2 cm or more long. Paleas translucent, glabrous or pubescent near the margins, usually slightly shorter than and partially enclosed by the lemmas. Stamens one or occasionally three in chasmogamous plants.

Anthers 0.3–1.5 mm long. Caryopses narrow, elongate, attenuate, flattened dorso-ventrally with the margins incurving at maturity; embryo small, one-fifth to one-tenth as long as the endosperm. Basic chromosome number, $x = 7$.

The separation of *Vulpia* from *Festuca* is based on a number of characters. With a few exceptions, the species of *Vulpia* are short-lived annuals, whereas those of *Festuca* are strong perennials. Typically the anthers of *Vulpia* are less than 0.5 mm long and the plants are cleistogamous. In *Festuca* the anthers are 3 mm or more long and the plants are chasmogamous. Species of *Vulpia* primarily are "weedy" grasses of disturbed habitats. In contrast, the festucas mainly are economically important grasses of meadows and pasturelands.

Key to the Species

First glume more than ½ the length of second glume.
- Lemma of lowermost floret 2.5–3.5 mm long, pubescent; caryopses 1.5–2.0 mm long. . . . . 2. *V. sciurea*
- Lemma of lowermost floret 3.5–7.5 mm long, pubescent, scabrous or glabrous; caryopses 2.5–5.5 mm long.
  - Spikelets with 5–11 (–17) florets; florets closely imbricate, with rachilla internodes typically 0.5–0.7 mm long; lemma awns 0.3–6.0 (–9.0) mm long. . . . . 1. *V. octoflora*
  - Spikelets with 1–5 (–7) florets, the florets not closely imbricate, with rachilla internodes usually 1 mm or more long; lemma awns 4–22 mm long.
    - Panicle branches and pedicels, at least the basal one, spreading or reflexed at maturity and with a callus in the branch axil. . . . . 3. *V. microstachys*
    - Panicle branches and pedicels appressed-erect or the branches spreading at the tips from an erect base; branches and pedicels all lacking axillary calluses. . . . . 4. *V. bromoides*

First glume less than 1/2 the length of second glume, usually much reduced and often rudimentary. . . . . 5. *V. myuros*

1. Vulpia octoflora (Walt.) Rydb., Bull. Torrey Bot. Club 36:528. 1909.

Annual with slender, weak, erect or decumbent culms, these mostly 10–60 cm tall, solitary, or loosely tufted. Culms and leaves glabrous or pubescent. Ligules 0.5–1.0 mm long. Blades narrow, flat, or involute, to 10 cm long, 0.5–1.0 mm broad, soon withering and turning brown. Panicles narrow, 1–20 cm long, with appressed, spicate or racemose branches or reduced to a spicate raceme. Spikelets with 5–17 florets, green or straw colored at maturity, laterally compressed, 4–10 mm long excluding the awns. Glumes subulate, the first 1-nerved, 1.7–4.5 mm long, the second 3-nerved, 2.7–6.7 mm long. Lemma of lowermost floret 2.7–6.5 mm long excluding the awn, lanceolate, glabrous, scabrous, or

pubescent, with an awn 0.3–6.0 (–9.0) mm long. Paleas translucent and pubescent near the margins, slightly shorter than the lemmas. Stamens one, occasionally three in chasmogamous plants. Anthers 0.3–1.5 mm long, borne on short filaments and usually clustered at the apex of the ovary between the two plumose stigmas. Caryopses brown at maturity, 1.7–3.3 mm long. Embryos about 0.3 mm long, inconspicuous.

Piper (1906) noted considerable variability in *Vulpia octoflora* but considered the differences between the variants too inconsistent for the recognition of more than two varieties. Fernald (1932), Steyermark (1963), and others have recognized a number of varieties, based on morphological divergence and geographical segregation. Some slight variation of general nature is apparent between plants and populations of *V. octoflora* in the Southeastern States and those of other regions of North America. In North Carolina, South Carolina, Georgia, and northern Florida, the plants tend to be more robust and the inflorescence more open than in populations of northern and western North America. The southeastern plants also have longer spikelets with more florets, longer caryopses, and quite consistently glabrous lemmas. Furthermore, the awn of the lowermost floret usually is longer.

Recognition of the following three varieties of *V. octoflora* is not entirely satisfactory. The characteristics of small spikelet size and short awns that provide the basis for the delimitation of var. *glauca* do not appear correlated in all cases. Depauperate plants of the Southwest with small spikelets fall within the range of var. *glauca* but the lemmas often are densely pubescent—the distinguishing characteristic of var. *hirtella*. Lemma indument often varies on spikelets of the same plant and even on different lemmas of the same spikelet.

Key to Varieties of Vulpia octoflora

Spikelets, excluding awns, mostly 4.0–5.5 mm long; awn of lowermost floret 0.3–3.0 mm long. . . . . 1B. var. *glauca*

Spikelets, excluding awns, mostly 5.5–10.0 mm long; awn of the lowermost floret 2.5–6.0 (–9.0) mm long.

Lemma glabrous or slightly scabrous on back, often scabrous on margins. . . . . 1A. var. *octoflora*

Lemma prominently long-scabrous to densely pubescent on back, at least near apex. . . . . 1C. var. *hirtella*

1A. Vulpia octoflora (Walt.) Rydb. var. octoflora.—*Festuca octoflora* Walt., Fl. Carol. 81. 1788. Type: South Carolina, Santee Valley, *Walter s.n.* The location of the type apparently is unknown. Piper (1906) stated that according to A. S. Hitchcock there is no specimen to represent this species in the part of Walter's herbarium preserved in the British Museum.—*Gnomia octoflora* (Walt.) Lunnell, Amer. Midl. Naturalist 4:224. 1915.

Festuca setacea Poir., Encyl. Suppl. 2:638. 1811. TYPE: South Carolina (?). Described from a plant grown in the Jardin du Val de Grace, France, the original source not definitely known. Piper (1906) did not locate the type nor have we done so.—*Diarrhena setacea* (Poir.) Roem. & Schult., Syst. Veg. 1:289. 1817.

Festuca parviflora Ell., Bot. So. Carolina & Georgia 1:170. 1816. TYPE: South Carolina, Orangeburg, *Mrs. J. S. Bennett s.n.* The type is at the College of Charleston *fide* Piper (1906); it was examined by Piper but not by us.

Festuca octoflora Walt. var. *aristulata* L. H. Dewey, Contr. U. S. Natl. Herb. 2:547. 1894. TYPE: "Dry hills throughout Texas and common throughout the southern United States". No collection cited.

Inflorescence with slender lower branches spreading at the tips or the branches all contracted and racemose. Spikelets 5.5–10.0 mm long, usually not or only slightly overlapping. Lemmas glabrous or somewhat short-scabrous near apex and on margins. Awn of lowermost floret 3–6 (–9) mm long. Caryopses 2.0–3.7 mm long.

DISTRIBUTION: Widespread throughout North America and introduced in temperate regions of South America, Europe, and Asia. Usually in disturbed habitats such as old fields, roadsides, ditches, and other areas where secondary plant succession is occurring. In North America, *V. octoflora* var. *octoflora* ranges from Connecticut to British Columbia and southward to Florida and Baja California. It is most commonly encountered from Virginia to northern Oklahoma and southward to northern Florida and the Texas Gulf Prairie.

1B. VULPIA OCTOFLORA (Walt.) Rydb. var. GLAUCA (Nutt.) Fern., Rhodora 47:104. 1945.—*Festuca tenella* Willd. var. *glauca* Nutt., Trans. Amer. Philos. Soc. 5:147. 1837. TYPE: Arkansas, Fort Smith, *Nuttall s.n.* (PH).—*Festuca octoflora* Walt. var. *glauca* (Nutt.) Fern., Rhodora 34:209. 1932.

Festuca tenella Willd., Sp. Pl. 1:419. 1797. TYPE: "Habitat in America boreali". Willdenow made no reference to a specific (type) collection.—*Schenonorus tenella* (Willd) Beauv., Ess. Agrost. 99, 163, 177. 1812.—*Brachypodium festucoides* Link, Enum. Pl. Hort. Berol. 1:95. 1821. Based on *Festuca tenella* Willd.—*Vulpia tenella* (Willd.) Heynh., Nom. 1:854. 1840.—*Festuca octoflora* Walt. var. *tenella* (Willd.) Fern., Rhodora 34:209. 1932.—*Vulpia octoflora* (Walt.) Rydb. var. *tenella* (Willd.) Fern., Rhodora 47:107. 1945.

Festuca gracilenta Buckl., Proc. Acad. Nat. Sci. Philadelphia 1862:97. 1862. TYPE: "Northern Texas", *Buckley s.n.* (PH).

Panicle branches usually appressed, only infrequently spreading at the tips. Spikelets mostly 4.0–5.5 mm long excluding the awns, subsessile or short-pediceled, closely arranged on main inflorescence axis and short branches. Lemmas glabrous or scabrous. Awn of lowermost floret 0.3–3.0 mm long.

DISTRIBUTION: Widespread in North America. Most frequent in southern Canada and the northern half of the United States, ranging from southern Quebec, Ontario, and British Columbia to northern Georgia and California. Variety *glauca* is the most common representative of *V. octoflora* from Maine and North Dakota to Virginia and western Kansas.

Fernald (1932) followed Nuttall in recognizing *V. octoflora* var. *glauca* as a varietal taxon, which he characterized as having crowded inflorescences, imbricated spikelets, and awns not more than 2 mm long. Fernald also proposed varietal status under *V. octoflora* for Willdenow's *Festuca tenella*. In the present study, however, the characteristics of *glauca* and *tenella* were found to vary and intergrade to such an extent that taxonomic recognition of the latter would be highly unsatisfactory.

Plants of many populations from the Texas Panhandle are intermediate in morphological characters between var. *octoflora* and var. *glauca*. In these plants the panicle branches are appressed, the spikelets are about 5.5 mm long and densely overlapping, and the awns of the lowermost florets are less than 3 mm long.

1C. VULPIA OCTOFLORA var. HIRTELLA (Piper) Henr., Blumea 2:320. 1937.—*Festuca octoflora* subsp. *hirtella* Piper, Contr. U. S. Natl. Herb 10:12. 1906. TYPE: Arizona, Pima Co., Santa Catalina Mts., *Shear 1962* (US).

Festuca pusilla Buckl., Proc. Acad. Nat. Sci. Philadelphia 1862:98. 1862. TYPE: "Upper California", *Nuttall s.n.* (PH).

Panicle branches appressed, densely-flowered, the spikelets closely overlapping. Spikelets mostly 5.5–10.0 mm long excluding the awns. Lemmas prominently scabrous to densely pubescent. Awn of lowermost floret 2.5–6.5 mm long.

DISTRIBUTION: British Columbia south to Oklahoma, Texas, and Baja California. This is the most common variety of *V. octoflora* in the Southwest. A few plants of southeastern U. S. with strongly scabrous lemmas have been referred to this taxon.

2. VULPIA SCIUREA (Nutt.) Henr., Blumea 2:323. — *Festuca sciurea* Nutt., Trans. Amer. Philos. Soc. 5:147. 1837. TYPE: Arkansas, *Nuttall s.n.*, in 1837 (PH).

?Festuca quadriflora Walt., Fl. Carol. 81. 1788. No known type or authentic specimen and description inadequate for determination of species. Not *Festuca quadriflora* Honck., 1782.

Festuca monandra Ell., Bot. So. Carolina & Georgia 1:170. 1816. Published as a synonym of *Festuca myuros* as misapplied by Elliot. In referring to the "hairy corolla" Elliott indicated that the plant he had in mind was *Vulpia sciurea.—Dasiola elliotea* Raf., Noegenyt. 4. 1825. Based on *Festuca monandra* Ell.—*Vulpia elliotea* (Raf.) Fern., Rhodora 47:106. 1945.

Culms 15–60 cm tall, erect or drooping at maturity. Herbage glabrous. Ligules 0.5–1.0 mm long. Blades flat or involute, usually less than 10 cm long and 0.5–1.0 mm broad. Panicles contracted, 5–20 cm long, with erect-appressed branches. Spikelets laterally compressed, 3.5–5.0 mm long excluding the awns, with 3–6 florets, the uppermost reduced. Glumes glabrous, subulate, the first 1-nerved, 1.3–2.5 mm long, the second obscurely 3-nerved, 2.5–4.0 mm long. Lemma of lowermost floret lanceolate, appressed-pubescent, 2.5–3.5 mm long excluding the awn. Awn of lowermost floret 4.5–9.5 mm long. Palea slightly shorter than the lemma. Stamens one, with an anther about 0.5 mm long on a short filament. Caryopses cylindrical and attentuate, 1.5–2.0 mm long, with a short, inconspicuous embryo.

Distribution: South on the eastern Coastal Plain from New Jersey and Delaware to northern Florida, southern Alabama and Mississippi, a few records from southern Iowa, northern Missouri and central Oklahoma, and many collections from the eastern half of Texas. *Vulpia sciurea* grows mostly in deep sandy soil of open woodlands, field borders and roadside ditches. It is perhaps the most distinct of the North American species of the genus, readily differentiated from other vulpias by its small spikelets and consistently pubescent florets. Although rather wide ranging, this species is neither abundant nor conspicuous in areas of occurence.

3. Vulpia microstachys (Nutt.) Benth., Pl. Hartw. 342. 1957.

Culms solitary or loosely tufted, glabrous or puberulent. Sheaths and blades glabrous or pubescent, the blades involute or less frequently flat, mostly 10 cm or less long and 0.5–1.0 mm broad. Ligules 0.5–1.0 mm long. Panicles narrow, 3–13 cm long, the branches and pedicels at first erect-appressed and then at least the lowermost typically spreading or reflexed in age; sometimes all pedicels and branches spreading or reflexed at maturity. Spikelets 4–9 mm long excluding the awns, often purple-tinged, with 1–6 florets, the uppermost reduced and inconspicuous. Glumes glabrous, scabrous, or pubescent, subulate, the first 1.7–5.5 mm long, the second 3.5–7.5 mm long. Lemma of lowermost floret (3.5–) 4.5–7.0 mm long excluding the awn, indistinctly 5-nerved, glabrous, scabrous or pubescent. Awn of lowermost floret (3–) 6–20 mm long. Palea usually slightly longer than body of lemma, tipped by 2 short, scabrous awns. Stamens usually 1, occasionally 3. Caryopses 3.5–5.5 mm long.

Several species have been delimited on the basis of populations herein interpreted as comprising *V. microstachys*. Piper (1906) recognized seven specific segregates, basing these on spikelet pubescence, the relative degree of spreading inflorescence branches, and the number of florets per spikelet. Hitchcock (1923, 1935) and Chase (1951) followed closely the concepts of Piper and recognized seven, eight, and nine

species respectively. The four varieties herein recognized all are differentiated on the basis of spikelet indument. The varieties commonly grow intermingled and intermediate, intergrading types are not infrequent.

Key to Varieties of Vulpia microstachys

Spikelets pubescent.
  Glumes or lemmas glabrous.
    Lemmas pubescent; glumes glabrous. . . 3A. var. *microstachys*
    Lemmas glabrous; glumes pubescent. . . . . 3C. var. *confusa*
  Glumes and lemmas pubescent. . . . . 3B. var. *ciliata*
Spikelets glabrous or scabrous. . . . . 3D. var. *pauciflora*

3A. Vulpia microstachys (Nutt.) Benth. var. microstachys.—*Festuca microstachys* Nutt., J. Acad. Nat. Sci. Philadelphia II, 1:187. 1848. Type: California, Los Angeles, *Gambel s.n.* The type has not been located; Piper (1906) noted that it is not at Kew nor in the Philadelphia Academy of Science.

Festuca microstachys Nutt. var. *subapressa* Suksdorf, Werdenda 1:3. 1923. Type: Washington, Klickitat Co., Bingen, *Suksdorf 6236* (lectotype in WS, isotypes in K, WS).

Festuca arida Elmer, Bot. Gaz. (Crawfordsville) 26:52–53. 1903. Type: Washington, Yakima, *Henderson 2196* (isotypes in US, WS).—*Vulpia arida* (Elmer) Henr., Blumea 2:323. 1937.

Panicle branches and pedicels all spreading or reflexed or only the basal ones spreading. Spikelets 4.5–7.5 mm long excluding the awns, with (1–) 2–5 florets. Glumes glabrous. Lemmas sparsely to densely pubescent.

Distribution: Occasional in loose soil on open slopes, ditchbanks and road rights of way, from northern Idaho, Washington, Oregon, and western Nevada to southern California.

Plants with inflorescence branches and pedicels only slightly spreading at maturity have been recognized as *Vulpia arida* (Elmer) Henr.

3B. **Vulpia microstachys** (Nutt.) Benth. var. **ciliata** (Beal) Lonard & Gould, comb. nov.—*Festuca microstachys* Nutt. var. *ciliata* Beal, Grasses N. Amer. 2:585. 1896. Not *Festuca ciliata* Danth. Type: Oregon, Grants Pass, *Howell s.n.* (holotype in MSC, isotype in US).—*Festuca microstachys grayi* Abrams, Fl. Los Angeles 52. 1904. Based on *Festuca microstachys* Nutt. var. *ciliata Beal.*—*Festuca pacifica* Piper var. *ciliata* (Beal) Hoover, Madroño 3:227. 1936.—*Festuca grayi* (Abrams) Piper, Contr. U. S. Natl. Herb. 10:14. 1906.—*Vulpia grayi* (Abrams) Henr., Blumea 2:323. 1937.

Festuca eastwoodae Piper, Contr. U.S. Natl. Herb. 10:16. 1906. Type: California, Monterey Co., Santa Lucia Mts., *Eastwood s.n.*, in 1897 (holotype in US).—*Vulpia eastwoodae* (Piper) Henr. Blumea 2:323. 1937.

Panicle branches and pedicels all spreading or reflexed or the upper ones erect. Florets usually 2–4. Glumes and lemmas sparsely or densely pubescent.

Distribution: In loose, sandy soils from central Washington through Oregon and California to northern Baja California and western Arizona.

This is the second most common variety of *V. microstachys* in California, exceeded in abundance and distribution only by var. *pauciflora*. Plants of forest openings in northern California with all branches and pedicels strongly reflexed or spreading and spikelets densely pubescent have been recognized as *Vulpia eastwoodae* (Piper) Henr.

3C. **Vulpia microstachys** (Nutt.) Benth. var. **confusa** (Piper) Lonard & Gould, comb. et stat. nov. — *Festuca confusa* Piper, Contr. U. S. Natl. Herb. 10:13. 1906. Type: Washington, Klickitat Co., *Suksdorf 1140* (holotype in US, isotypes in UC, WS). — *Vulpia confusa* (Piper) Henr., Blumea 2:323. 1937.

Festuca suksdorfii Piper ex Suksdorf, Werdenda 1:2. 1923. Type: Washington, Klickitat Co., Bingen, *Suksdorf 5604* (lectotype and isotype in WS).

Festuca tracyi Hitchc. in Abrams, Illustr. Fl. Pacific States 1:220. 1923. Type: California, Napa Co., *Tracy 1479* (isotypes in CAS, UC). —*Vulpia tracyi* (Hitchc.) Henr., Blumea 2:323. 1937.

Panicle branches and pedicels all spreading or reflexed at maturity or the upper ones erect.

Distribution: Occasional on sandy, open sites from southern Washington to southern California.

Vulpia microstachys var. *confusa* apparently is the least abundant of the four *V. microstachys* varieties. A form with all branches and pedicels widely spreading or reflexed was described by Hitchcock as *Festuca tracyi*.

3D. **Vulpia microstachys** (Nutt.) Benth. var. **pauciflora** (Beal) Lonard & Gould, comb. nov.—*Festuca microstachys pauciflora* Beal, Grasses N. Amer. 2:586. 1896. Type: Oregon, *Howell s.n.*

Festuca reflexa Buckl., Proc. Acad. Nat. Sci. Philadelphia 1862:98. 1862. Type: "Upper California", *Nuttall s.n.* (PH).—*Vulpia reflexa* (Buckl.) Rydb., Bull. Torrey Bot. Club 36:538. 1909.

Festuca pacifica Piper, Contr. U. S. Natl. Herb. 10:12. 1906. Type: Washington, Whitman Co., Pullman, *Elmer 262* (US).—*Vulpia pacifica* (Piper) Rydb., Bull. Torrey Bot. Club 36:535. 1909.

Festuca subbiflora Suksdorf, Werdenda 1:2. 1923. Type: Washington, Klickitat Co., *Suksdorf 6144* (lectotype in WS, isotypes in CAS, K, WS), *10299* (CAS, K), and *1298*.

Festuca dives Suksdorf, Werdenda 1:3. 1923. Not *Festuca dives* Muell., 1863. Type: Washington, Klickitat Co., Bingen, *Suksdorf 6153* (lectotype in WS, isotypes in CAS, WS).

Festuca pacifica Piper var. *simulans* Hoover, Madroño 3:228. 1936. TYPE: California, Kern Co., Blackwells Corner, *Hoover 451* (UC). —*Festuca microstachys* Nutt. var. *simulans* (Hoover) Hoover, Leafl. W. Bot. 10:338–339. 1966.

Panicle branches and pedicels all spreading or reflexed or the upper ones erect. Spikelets with 1–6 florets.

DISTRIBUTION: On sandy, often disturbed sites from British Columbia and western Montana southward to Arizona and Baja California.

This is the most common and widespread variety of the species. It often grows intermingled with plants of the other varieties. Differences in spikelet indument among the four varieties usually are in sharp contrast but intermediacy is expressed in some populations, both in respect to length and density of hairs or spicules. Specimens of the type collection of *Festuca divis* have short- to long scabrous lemmas and thus are essentially intermediate between the varieties *pauciflora* and *ciliata*. The name *Vulpia reflexa* has been applied to plants with sharply reflexed, 1–2 (–3) -flowered, glabrous spikelets. Difficulty is experienced in the separation of immature or atypical plants of *V. microstachys* var. *pauciflora* and *V. bromoides*. In southern California and Baja California, differences between var. *microstachys* and *V. octoflora* var. *octoflora* are not always apparent.

4. VULPIA BROMOIDES (L.) S.F. Gray, Natur. Arrange. Brit. Plants 124. 1821.—*Festuca bromoides* L., Sp. Pl. 1:75. 1753. TYPE: Italy, "In Anglia Gallia".

Bromus dertonensis All., Fl. Pedem 2:249. 1785. TYPE: Italy, *Scheuchzer s.n.*—*Festuca dertonensis* (All.) Asch. & Graebn., Syn. Mittleleur. Fl. 2:588. 1900.—*Vulpia dertonensis* (All.) Gola, Malpighia 18:366. 1904.

Festuca sciuroides Roth, Bet. Abh. & Beobacht. 43. 1787. TYPE: Germany.—*Vulpia sciuroides* (Roth) K.C. Gmelin, Suppl. Fl. Baden 66. 1826.

Culms solitary or loosely tufted, erect or decumbent at base, glabrous or minutely retrorsely scabrous-pubescent, 5–50 cm tall. Leaves glabrous or puberulent. Ligules about 0.5 mm long. Blades flat or involute, mostly less than 15 cm long and 0.5–2.5 mm broad. Panicles contracted, 5–15 cm long, the branches usually tightly erect-appressed; panicles conspicuously exserted above uppermost leaf, the inflorescence stalk extending as much as 15 cm long below the lowermost branches. Pedicels flattened or noticeably clavate above. Spikelets 5–10 mm long excluding the awns, with 4–7 florets, the uppermost reduced; nodes of rachilla about 1 mm apart, the florets appearing widely spaced. Glumes glabrous, subulate, the first 3.5–5.0 mm long, the second 4.5–7.0 mm long. Lemma of lowermost floret (4.0–) 5.5–8.0 mm long excluding the awn, glabrous and lustrous or scabrous. Awn of lowermost floret 3–12 mm long, firm,

scabrous. Palea about as long as lemma. Stamens usually one, with an anther about 0.5 mm long. Caryopses 3.5–4.0 mm long.

DISTRIBUTION: In temperate regions of the world, common throughout Europe. *Vulpia bromoides* is adventive or naturalized in North and South America and is an introduced "weedy" grass of high altitudes in tropical Africa. In North America it is most common on the west coast where it ranges from British Columbia to northern Baja California. It occurs sparingly in other regions of North America.

Vulpia bromoides is similar in general habit and spikelet characteristics to *V. myuros* but is readily distinguished by the longer first glume. As has been noted, immature or depauperate specimens can be confused with similarly atypical plants of *V. microstachys* var. *pauciflora*.

5. VULPIA MYUROS (L.) K. C. Gmelin, Fl. Baden. 1:8. 1805.

Culms solitary or loosely tufted, erect or ascending from a decumbent base, glabrous, 10–60 (–90) cm tall. Sheaths glabrous or the lowermost puberulent, broadly rounded and often lobed laterally at apex, abruptly narrowing to and continuous with a fimbriate ligule less than 0.5 mm long. Blades long or short, flat or more commonly involute, often filiform, mostly 15 cm or less long and 0.5–3.0 mm broad, usually glabrous on abaxial surface and thinly puberulous on adaxial surface, at least near base. Inflorescence a contracted, often rather dense panicle or spicate raceme 3–25 cm long, often not completely exserted from sheath at maturity; panicle branches erect-appressed or drooping. Spikelets 5.5–12.0 mm long excluding the awns, with 3–7 florets. Glumes thin, glabrous, subulate, the first mostly 0.5–2.5 mm long, the second 3-nerved, 2.3–5.5 mm, at least twice as long as the first. Lemma of lowermost floret 4.5–7.0 mm long excluding the awn, usually scabrous above; lemma awns 7.5–22.0 mm long. Palea about as long as lemma, membranous, colorless, glabrous. Stamens usually 1, the anther about 0.5 mm long. Caryopses 3.0–4.5 mm long.

KEY TO VARIETIES OF VULPIA MYUROS

Lemmas not ciliate on margins near apex; awn of lowermost floret 7.5–17.0 mm long. . . . . 5A. var. *myuros*

Lemmas ciliate on margins near apex; awn of lowermost floret 9.5–22.0 mm long. . . . . 5B. var. *hirsuta*

5A. VULPIA MYUROS (L.) K. C. Gmelin var. MYUROS.—*Festuca myuros* L., Sp. Pl. 74. 1753. TYPE: "Habitat in Anglia (England), Italia".—*Distomischus myuros* (L.) Dulac, Fl. Haut. Pyr. 91. 1867.—*Zerna myuros* (L.) Jacks., Ind. Kew 2:1249. 1895.—*Avena muralis* Salisb., Prodr. Stirp. 22. 1796. Based on *Festuca myuros* L.

DISTRIBUTION: Throughout the temperate-subtropical regions of the world. This is the most widely distributed *Vulpia*. It probably is native to central Europe but occurs as a common weed throughout southern

Europe, North and South Africa, the Orient, Australia, and North and South America. In Canada, the United States, and Mexico it is most frequent in coastal regions.

Vulpia myuros var. *myuros* appears closely related to *V. bromoides* from which it is distinguished primarily by the greatly reduced first glume. Hubbard (1968) reported a suspected hybrid between *V. myuros* var. *myuros* and *Festuca rubra* in the British Isles.

5B. Vulpia myuros (L.) K. C. Gmelin var. hirsuta Hack., Cat. Gram. Port. 24. 1880. Type: Portugal, "Coimbra". — *Festuca myuros* L. var. *hirsuta* (Hack.) Asch. & Graebn., Syn. Mitteleur. Fl. 2:588. 1901.

Festuca megalura Nutt., J. Acad. Nat. Sci. Philadelphia 2(1):188. Type: California, Santa Barbara, *Gambel s.n.* Location of type not known; Piper (1906) stated ". . . we have been unable to locate it in any American herbarium nor is it in the British Museum."—*Vulpia megalura* (Nutt.) Rydb., Bull. Torrey Bot. Club 26:538. 1909.

Distribution: In many cool, temperate, and warm regions of the world including Europe, North and South America, the Hawaiian Islands, Japan, and Australia. In North America this taxon is most frequent along the west coast from central Alaska to Baja California. It is occasional throughout the Rocky Mountain area and Midwest and there are a few records from eastern states including Pennsylvania, South Carolina, Alabama, and Mississippi.

Plants of this taxon do not appear to be native to the United States as was assumed by Piper (1906), Hitchcock (1935), and others. *Vulpia myuros* var. *myuros* and *V. m.* var. *hirsuta* frequently grow intermingled in East Texas and herbarium collections often contain mixtures of the two varieties. Many California specimens of var. *hirsuta* are only sparsely ciliate on the lemma margins. Some European plants of var. *hirsuta* have lemmas that are much more conspicuously ciliate than those of North America plants and some reportedly have lemmas that are pubescent on the back as well as the margins. Plants grown at the Royal Botanic Gardens, Kew, England, from seed collected at the type locality, Coimbra, Portugal, were observed to have essentially the same lemma characteristics as the North American populations.

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Literature Cited

Bews, J. G. 1929. The world's grasses, their differentiation, distribution, economics, and ecology. Longmans Green and Co. Ltd., London.

Bowden, W. M. and H. A. Senn. 1962. Chromosome numbers in 28 grass genera from South America. Canad. J. Bot. 40:1115–1122.

Chase, A. 1951. *In* Hitchcock, Manual of the grasses of the United States. Second edition, revised. U. S. Dept. Agric. Misc. Publ. 200.

Chippendall, L. K. A. 1955. A guide to the identification of grasses in South Africa (part 1 of The grasses and pastures of South Africa). Cape Times Limited, Parow, C. P.

Fernald, M. L. 1932. Notes on *Festuca octoflora*. Rhodora 34:209–211.

———. 1945. Botanical specialties of the Seward forest and adjacent areas of southeastern Virginia. Rhodora 47:93–142.

———. 1950. Gray's manual of botany. Eighth edition. American Book Co., New York.

Gould, F. W. 1958. Chromosome numbers in southwestern grasses. Amer. J. Bot. 45:757–767.

———. 1960. Chromosome numbers in southwestern grasses. II. Amer. J. Bot. 47:873–877.

———. 1966. Chromosome numbers of some Mexican grasses. Canad. J. Bot. 44:1683–1696.

Hedberg, O. 1957. Afroalpine vascular plants. Symb. Bot. Upsal. 15:1–41.

Henrard, J. T. 1937. A study of the genus *Vulpia*. Blumea 2:299–326.

Hitchcock, A. S. 1923. Gramineae *in,* W. L. Jepson, Manual of the flowering plants of California. Associated Students Store, U. of California, Berkeley.

———. 1935. Manual of the grasses of the United States. U. S. Dept. Agric. Misc. Publ. 200.

Hubbard, C. E. 1968. Grasses: A guide to their structure, identification, uses and distribution in the British Isles. Penguin Books, Ltd., Harmondsworth, Middlesex.

Litardiere, R. De. 1950. Nombres chromosomiques de diverses Graminees. Bol. Soc. Brot. (second series) 24:79–87.

———. 1956. *In* C. D. Darlington and A. P. Wylie. Chromosome atlas of flowering plants. Macmillan Co., New York.

Lonard, R. I. 1970. A biosystematic study of the genus *Vulpia* (Gramineae). Ph. D. Dissertation: Texas A&M University, College Station.

Löve, A. and D. Löve. 1948. Chromosome numbers of northern plant species. Reykjavik Atvinnudeild Haskolans. Rit. Landbunaardeil dar, B-flokkur 3.

Metcalfe, C. R. 1960. Anatomy of the monocotyledons. Vol. 1. The Gramineae. Clarendon Press, Oxford.

Myers, W. M. 1947. Cytology and genetics of forage grasses. Bot. Rev. (Lancaster) 13:318–421.

Niehaus, T. F. 1961. A taxonomic and cytologic investigation of the *Festuca microstachys* complex. M. A. Thesis: Univ. California, Davis.

Parodi, L. R. 1956. Las especies de gramineas del genero *"Vulpia"* de la Argentina y paises lamitrofes. Revista Argent. de Agron. 23:71–94.

Paunero, E. 1964. Notas sobre gramineas. II. Consideraciones acerca de las especies espanolas del genero *Vulpia* Gmel. Anales Inst. Bot. Cavanilles 22:82–114.

Piper, C. V. 1906. North American species of *Festuca*. Contr. U. S. Natl. Herb. 10:1–48.

Rosengurtt, B., B. R. Arrillago De Maffei, and P. Izaguirre De Artucio. 1970. Gramíneas Uruguayas. Universidad de la Republica, Departamento de Publicaciones, Montivideo.

Stahlin, A. 1956. *In* C. D. Darlington and A. P. Wylie. Chromosome atlas of flowering plants. Macmillan Co., New York.

Steyermark, J. A. 1963. Flora of Missouri. Iowa State Univ. Press, Ames.